LATE WISCONSINAN APPALACHIAN HERPETOFAUNAS: RELATIVE STABILITY IN THE MIDST OF CHANGE

LESLIE P. FAY[1]

ABSTRACT

Fossil herptiles from eastern North America exhibit less dramatic Wisconsinan-Holocene range adjustments than many contemporaneous mammals, birds, and plants. Mammal and bird faunal lists consist of current residents of the fossil locality plus a sizeable component of taxa that ranges to the north or west. Herptile lists include area residents with a few forms now removed to the south. Factors responsible for the varying responses to climatic change between and within vertebrate classes have not yet been adequately addressed. Most Late Wisconsinan Appalachian herpetofaunas neither support nor contradict the climatic equibility hypothesis, because herptiles are either insensitive to climatic and biotic change or an appropriate transfer function has not been formulated to provide a partial climatic analog. Although range limits of many plants and animals changed by hundreds of kilometers in response to the late glacial-interglacial climatic shift, herptiles in eastern North America seem to have been less strongly affected by these events. Previously reported extralimital records of *Masticophis flagellum, Crotalus adamanteus* (Natural Chimneys, Virginia), and *Bufo americanus copei* (New Paris No. 4, Pennsylvania) are rejected.

INTRODUCTION

Until the last twenty years, environmental reconstructions developed from fossil evidence depended on the assumption that current (i.e. before human disturbance) patterns of plant communities existed through most of the Quaternary Period. With allowances for areas covered by glacial ice and perhaps a severe "periglacial" fringe, the modern communities were mapped as if they migrated intact north and south in response to glacial-interglacial cycles (cliseral shift model: Brunnschweiler, 1962; Dansereau, 1957; Dillon, 1956; Flint, 1971; Martin, 1958). The boundaries of these dislocated communities were delineated on scanty pollen evidence with no radiometric time frame and were fortified by individual large vertebrate discoveries. As data points were few and non-uniformly spaced, much of this early reconstruction was based on inference. Animals now associated with each community were assumed to have moved along with the plants (Martin, 1958).

The use of screen-washing techniques for recovering smaller macroscopic fossils (Hibbard, 1949; McKenna, 1962) has made it possible to utilize small animals in paleoenvironmental reconstructions. Small animals are often more closely linked to microhabitat than are large forms and less likely to migrate long distances through anomalous habitats. Careful stratigraphic documentation makes it feasible to distinguish synchronously deposited and heterochronic fossil accumulations when each contains species not now sympatric.

The distribution of many small animals was markedly altered by glacial advances and retreats. Discovery and analysis of many local faunas and pollen profiles has demonstrated that these changes in distribution did not occur as entire community (cliseral) shifts, but as responses by individual species of plants (e.g.,

[1] San Bernardino County Museum, Redlands, CA 92374.

Davis, 1976) and animals (e.g. Graham, 1985) according to tolerance limits and interactions during climate-driven dissolution and reformation of communities (Graham and Lundelius, 1984).

The new interpretation of Quaternary environmental response is based mainly on information from the pollen and mammal fossil record. Comparatively little information has been reported on fossil herptiles (reptiles and amphibians), although they have been noted in eastern North American Quaternary local faunas for almost 90 years (e.g. Cope, 1899). Herptiles were simply listed in many papers with little or no interpretation and evaluation. Previous reviews of Quaternary climatic effects on herptiles relied almost solely on evidence from present distribution and speciation (i.e., morphologic differentiation between living taxa) (Auffenberg and Milstead, 1965; Blair, 1965; Schmidt, 1938; Smith, 1957). Twenty years ago, the fossil record was as yet so poorly known that ". . . the best we can hope for is to determine the relation to present distribution and present evidence of speciation to major shifts in climatic conditions" (Blair, 1965:543). Fortunately, the fossil record has since provided a number of herpetofaunas that can be used to study climatic conditions more directly. The suitability of fossil herptiles as climatic proxies (Bryson, 1985) has not been thoroughly evaluated. Although this study indicates they may not serve well as paleoclimatic indicators, further examination of modern herptile ecology in regard to the fossil record will be necessary to determine if a transfer function (Bryson, 1985) can be formulated.

Herpetofaunas from Frankstown Cave, New Paris No. 4, Natural Chimneys, Clark's Cave, Baker Bluff Cave, and Kingston Saltpeter Cave (Fig. 1) were chosen for this study because their relatively high species diversity suggested the potential for meaningful comparison with co-occurring mammals and birds previously reported. In prior studies, the finding of temperate and even supposedly austro-riparian herptiles in several of these local faunas contradicted the presence of boreal mammal and bird taxa. This apparent anomaly implies either: (1) The herptiles "leaked" into the deposits after the boreal + temperate mammal and bird accumulations, resulting in a heterochronic assemblage. Two corollaries are (i) no herptiles were present when the mammals and birds accumulated, or (ii) herptiles were present but did not fossilize (Fay, 1986). (2) The anomaly shows that herptiles responded differently to climatic change than did the more boreal mammal and bird taxa.

Two main objectives of this study are to (1) document regional relationships among central and southern Appalachian herptiles at the close of the most recent glaciation, and (2) compare inferred climatic effects on the herptiles with previously interpreted effects on mammals and birds.

PROCEDURES

All materials except that from Kingston Saltpeter Cave were collected by field parties directed by the Section of Vertebrate Fossils, The Carnegie Museum of Natural History, and are housed at that institution. Kingston specimens were collected by the Kingston Saltpeter Cave Study Group, Clayton County Cavers, National Speleological Society Grotto No. 285, and are reposited at Berry College, Rome, Georgia. Details of field sampling procedures can be found in the primary references for each locality cited in the Annotated Faunal Lists. Modern skeletal specimens of the Herpetology and Ichthyology Division, Michigan State University Museum, were used for comparative study of the fossils.

Explanations of identification methods are provided in the Selected Systematic Accounts for new or modified techniques. Both qualitative and quantitative morphometric methods were employed for identifying the fossils, because each is not entirely reliable alone. Taxonomy above the generic level follows Dowling and Duellman (1978). Genera, species, common names, and geographic distributions are after Conant (1975), Martof et al. (1980), and McCoy (1982).
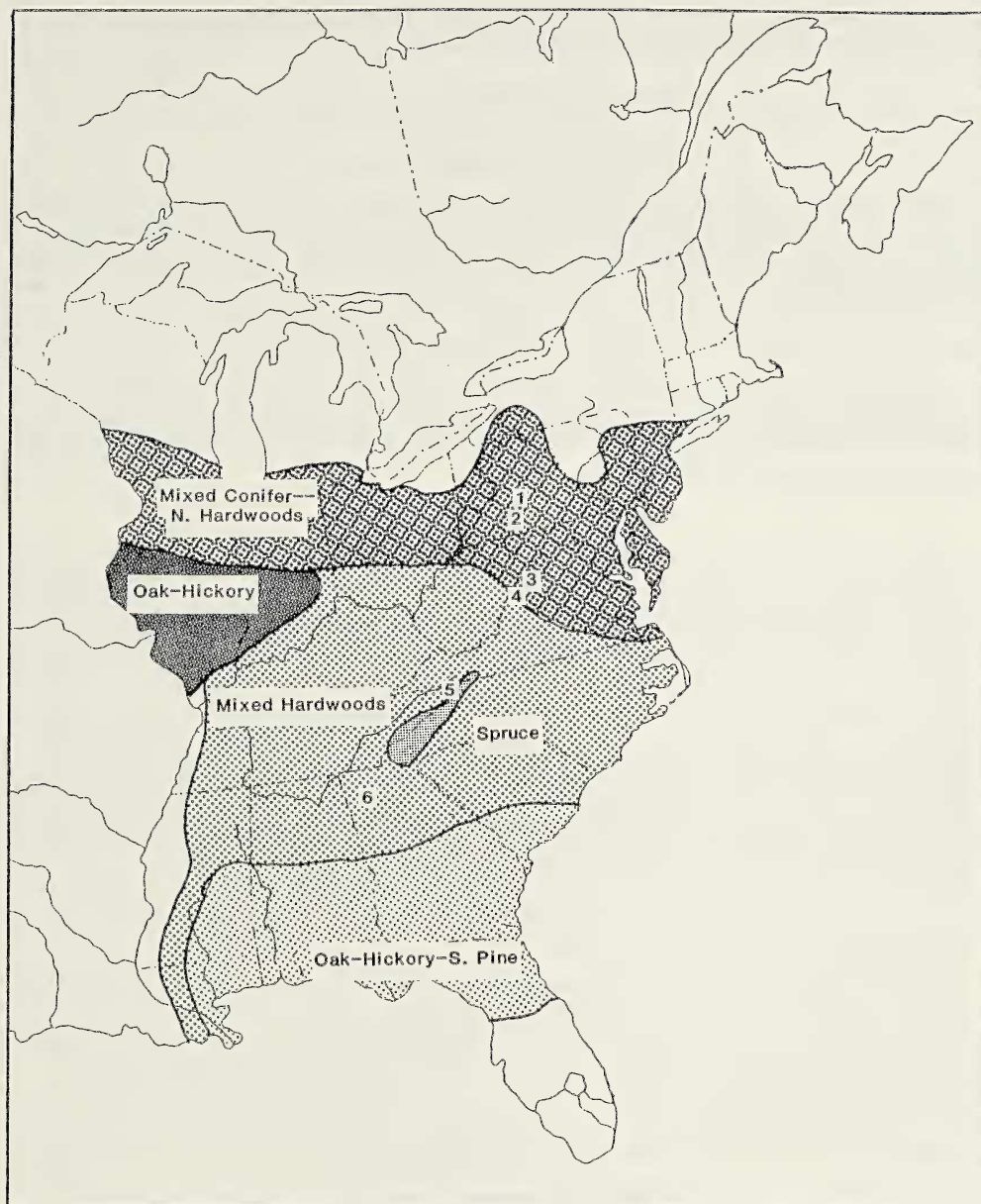
Fig. 1.—Location of six Late Wisconsinan–early Holocene local faunas in the central and southern Appalachian region. Base map illustrates selected paleovegetation units of 10,000 yr BP (after Delcourt and Delcourt; 1981:149, Fig. 7). 1—Frankstown Cave, PA; 2—New Paris Sinkhole No. 4, PA; 3—Natural Chimneys, VA; 4—Clark's Cave, VA; 5—Baker Bluff Cave, TN; 6—Kingston Saltpeter Cave, GA.

Abbreviations

BB—Baker Bluff Cave, CC—Clark's Cave, CL—centrum length, FC—Frankstown Cave, KSC—Kingston Saltpeter Cave, NAW—neural arch width, NC—Natural Chimneys, NP4—New Paris No. 4, NSH—neural spine height, NSL—

neural spine length, POPR—postzygopophysis to prezygopophysis length, PRPR—prezygopophysis width, ZW—zygosphene width.

SELECTED SYSTEMATIC ACCOUNTS

Class Amphibia
Family Plethodontidae

Many plethodontid taxa are difficult to distinguish when alive and may well prove impossible to separate as disarticulated fossils. Trunk vertebrae of the two subfamilies and several plethodontine genera and species may be identified with relative certainty.

Subfamily Desmognathinae

Occurrence.—NP4, NC, CC, BB, KSC.
The dusky salamanders occasionally have been elevated to family rank on the basis of characteristic opisthocoelous vertebrae (Soler, 1950). Attempts at specific determinations have not been successful.

Subfamily Plethodontinae

This subfamily includes all non-desmognathine plethodontids. Two genera, *Gyrinophilus* and *Pseudotriton,* have distinctive "false opisthocoelous" vertebrae (Soler, 1950:463). The remaining eastern North American plethodontines have not previously been thoroughly examined for distinctive osteological morphology that would allow identification of disarticulated fossils to the species level. Size and geographic range have been used for identifications (e.g., Holman, 1967; Lundelius, 1967; Richmond, 1964; Richmond in Guilday et al., 1964) but, as with desmognathines, a great deal of overlap exists between taxa. Members of the genus *Eurycea* may be distinguished by the characters listed below, and the remaining plethodontines are informally grouped as "*Plethodon*-type," including *Aneides, Hemidactylium,* and *Plethodon* in the region of this study.

Eurycea sp.

Occurrence.—NP4, NC, CC, KSC.
Eurycea vertebrae may be distinguished by a tendency toward the false opisthocoelous condition, well-separated transverse processes, condyle situated ventrally on the centrum, and with neural spine extending almost full length of the centrum. Species determination of fossil vertebrae has not yet been attempted.

Order Anura

Family Bufonidae
Bufo americanus Holbrook

Occurrence.—FC, NP4, NC, CC, BB, KSC.
B. americanus ilia may be distinguished by the broad base of the ilial prominence in lateral view (Holman, 1967). The dorsal protuberance is oriented anterodistally in mature *B. americanus,* but perpendicular to the longitudinal axis of the ilial shaft in other eastern North American *Bufo. B. americanus* ilia that exceed the modern size range for the species have been reported from Ladds Quarry, Georgia (ilial acetabular height 16.5 mm; Holman, 1967:157, Table 1). Kingston Saltpeter Cave, located about 13 km from Ladds, yielded the largest ilium in this study with acetabular height 8.8 mm. *Bufo americanus* osteology is extremely variable

in the morphological details relied upon for fossil identifications and a comprehensive examination of both modern and fossil specimens throughout the distribution is needed.

Bufo americanus copei was identified by Richmond (in Guilday et al., 1964) from New Paris No. 4. The subspecific determination was based on small size and association with boreal mammals. I have repeated this listing with strong reservation because of the need for morphological study already mentioned. Another small subspecies, *B. a. charlesmithi*, also exists, although in the southwest portion of the species range, rather than the northern fringe, where *B. a. copei* occurs (Conant, 1975:404, Map 261). Size and co-occurrence with extralimital mammals are insufficient criteria for subspecific identification of fossils. Cook (1984) does not support subspecific status for *B. a. copei* because of the wide zone of intergrading characters with the nominate subspecies.

The New Paris fossil ilia likely represent small, but mature *B. a. americanus,* the zoogeographic implications of which would accord with the rest of the herpetofauna.

Family Hylidae
Hyla chrysoscelis/versicolor

Occurrence. —FC.
Grey treefrogs are distinguished by call rates and chromosome counts, but no osteological criteria have been delineated that separate the two species.

Hyla crucifer (Wied)

Occurrence. —FC, NP4, CC, KSC.
The New Paris *H. crucifer* represent individuals larger than known modern specimens in snout–vent length by 5 mm (Lynch, 1966). Irvingtonian *H. crucifer* from Cumberland Cave, Maryland (Lynch, 1966) and all other specimens of this study are within modern size range. The paleoenvironmental significance of clinal variability for many Appalachian herptiles requires additional study. *Hyla* previously reported from Natural Chimneys and Baker Bluff Cave (one ilium each) have been re-identified as *Scaphiopus holbrooki* and juvenile *Bufo* sp., respectively.

Family Ranidae
Rana pipiens-group

Occurrence. —FC, NP4, NC, CC, KSC.
No method has been devised that adequately separates ilia of the leopard frog complex (Holman, 1977a). This group includes at least four parapatric species in eastern North America, distinguished by soft anatomy and call rates (Conant, 1975).

Class Reptilia
Order Testudines
Family Emydidae
?*Clemmys insculpta* (Le Conte) or
?*Pseudemys concinna* (Le Conte)

Occurrence. —KSC.
A badly eroded proximal left humerus resembles both *C. insculpta* and *P. concinna* in size and gross morphology but is not distinguishable. Both turtles are present in the Ladds Quarry local fauna (Holman, 1967, 1985a). If the specimen

is indeed a *C. insculpta* humerus, it is the only extralimital herptile occurrence at Kingston Saltpeter Cave.

Order Squamata
Suborder Serpentes

Snake vertebrae present an intricate and often frustrating exercise in identification. A large comparative collection is necessary, for the vertebrae are not only morphologically diverse, but variable among and within taxa and individuals.

Only mid-trunk vertebrae were used for identification in this study because adequate criteria are unknown for identifying anterior trunk and caudal vertebrae. Guidelines offered by Holman (1981) were used to separate subfamily groups. Calculation of vertebral mensural ratios, pioneered by Auffenberg (1963) and expanded by Meylan (1982) was utilized along with qualitative characters.

Family Colubridae
Subfamily Natricinae

This subfamily may be divided on the basis of vertebral size. *Seminatrix, Storeria, Tropidoclonion,* and *Virginia* vertebrae are less than 3 mm CL. Larger natricine vertebrae can be separated according to length-width ratios. *Thamnophis* vertebrae have CL/NAW ratios greater than 1.75. For *Clonophis, Nerodia,* and *Regina,* this ratio is less than or equal to 1.5.

?*Regina septemvittata* (Say)

Occurrence.—NP4, NC, CC.

Most members of the genus *Regina* have vertebral characters intermediate between my "small" and "large" natricine forms. According to these criteria of vertebral ratios and morphologic characters, *R. septemvittata* closely resembles the genus *Thamnophis,* except that the former has more abbreviated neural spines (Auffenberg, 1963) and blunter accessory processes. It is otherwise difficult to separate these two taxa.

Storeria dekayi (Holbrook)

Occurrence.—NP4, NC, CC, KSC.

Storeria occipitomaculata (Storer)

Occurrence.—NP4, NC, CC.

Storeria may be confused with *Virginia. Storeria* has NSL/ZW ratios averaging greater than 1.10, *Virginia* less than 1.05 (Auffenberg, 1963:192, table 21). *S. dekayi* can be very difficult to distinguish from *S. occipitomaculata.* Three ratios in combination have proven useful (*S. occipitomaculata* values in parentheses): POPR/CL > 1.08 (<1.07); NSL/ZW < 1.17 (>1.17); CL/NAW <1.91 (>1.94).

Thamnophis brachystoma (Cope)

Occurrence.—FC.

T. brachystoma vertebrae are distinguished from other small (<5 mm CL) natricines by taller neural spines, CL/NAW of 1.55–1.75, and POPR/PRPR of 1.00 to 1.03.

Virginia striatula (Linné)

Occurrence.—NC, CC, KSC.

Virginia valeriae Baird et Girard

Occurrence.—FC, NP4, NC, CC, KSC.

Vertebral ratios serve to distinguish the two *Virginia* species (*V. valeriae* values in parentheses): POPR/NAW > 2.00 (<1.75); CL/NAW > 1.77 (<1.55); NSL/ZW > 0.97 (<0.74).

Subfamily Colubrinae
Coluber or *Masticophis*

Occurrence.—NP4, NC, CC, BB, KSC.

I have discovered no reliable criteria to separate vertebrae of *Coluber* and *Masticophis,* although Meylan (1982) has had some success. Holman's (1981) cautionary note regarding *M. flagellum* determinations where sympatric with *Coluber* or other *Masticophis* is heeded. Until distinguishing features are discerned, I prefer to assign large colubrine vertebrae to "*Coluber* or *Masticophis.*" For this reason, I reject Richmond's determination of *M. flagellum* (in Guilday, 1962) for Natural Chimneys material.

Subfamily Lampropeltinae
Elaphe guttata (Linné)

Occurrence.—NP4, NC, CC, KSC.

Elaphe obsoleta (Say)

Occurrence.—NP4, NC, CC, KSC.

Auffenberg (1963:181, fig. 29) separated vertebrae of *E. obsoleta* from *E. guttata* by NSH/NSL ratio *versus* CL. Meylan (1982:33, table 6) achieved about 90% accuracy separating the two species by means of four length/width ratios. Also, in anterior view, the accessory processes of *E. obsoleta* are laterally directed, while those of *E. guttata* are slightly dorsolaterally directed.

Lampropeltis calligaster (Harlan)

Occurrence.—NP4, CC, KSC.

Lampropeltis getulus (Linné)

Occurrence.—NP4, NC, CC, BB, KSC.

Lampropeltis triangulum (Lacépède)

Occurrence.—NP4, NC, CC, BB, KSC.

L. calligaster may be separated from *L. triangulum* by the distinctly lower neural spines and anteriolateral direction of the accessory processes in the latter. *L. getulus* has the most strongly developed subcentral ridges among lampropeltines (Auffenberg, 1963). It most closely resembles *L. calligaster,* which has a haemal keel that does not widen toward the condyle as in *L. getulus* (Auffenberg, 1963). *L. getulus* also has shorter vertebrae with more pronounced dorsoventral flattening of the accessory processes than in *L. calligaster.*

Lampropeltinae, indeterminate

Occurrence.—FC.

Richmond (1964) tentatively assigned nine juvenile vertebrae to *L. triangulum.* I do not consider it prudent to assign such young specimens to species although they are certainly lampropeltines.

Table 1.—*Checklist of herptiles from six late Wisconsinan–early Holocene Appalachian local faunas.*

Taxon	Locality					
	FC	NP4	NC	CC	BB	KSC
Cryptobranchus alleganiensis					X	
Necturus maculosus					X	
Notophthalmus viridescens	X	X	X	X		X
Ambystoma maculatum-group		X	X	X	X	X
Ambystoma opacum-group			X	X	X	X
Ambystoma tigrinum			X			X
Ambystoma sp.	X	X		X	X	
Desmognathinae		X	X	X	X	X
Gyrinophilus porphyriticus			X	X		
Pseudotriton ruber						X
Pseudotriton sp.		X	X	X		
Eurycea sp.		X	X	X		X
Plethodon-type		X	X	X		X
Scaphiopus holbrooki			X	X		X
Bufo americanus	X	X	X	X	X	X
Bufo americanus ?copei		X				
Bufo woodhousei fowleri		X	X	X	X	X
Bufo sp.	X					
Hyla chrysoscelis/versicolor	X					
Hyla crucifer	X	X		X		X
Gastrophyrne carolinensis						X
Rana catesbeiana			X	X		X
Rana clamitans		X	X	X		
Rana palustris		X	X	X		
Rana pipiens-group	X	X	X	X		X
Rana sylvatica	X	X	X	X	X	
Rana sp.	X					X
Chelydra serpentina			X			
Kinosternidae						X
Chrysemys picta						X
Clemmys insculpta	X					?
Graptemys geographica				X		
Pseudemys sp.						X
Terrapene carolina			X			X
Anolis carolinensis						X
Sceloporus undulatus			X	X		X
Eumeces fasciatus					X	
Eumeces ?laticeps				X		
Scincella lateralis			X			X
Nerodia ?erythrogaster			X			
Nerodia sipedon	X	X	X	X	X	X
Nerodia sp.					X	
?Regina septemvittata		X	X	X		
Storeria dekayi		X	X	X		X
Storeria occipitomaculata		X	X	X		
Storeria sp.						X
Thamnophis brachystoma	X					
Thamnophis ?sauritus		X		X		X
Thamnophis sirtalis	X	X	X	X	X	X
Thamnophis sp.		X	X		X	
Virginia striatula			X	X		X
Virginia valeriae	X	X	X	X		X
Carphophis amoenus	X	X	X	X		X
Diadophis punctatus	X	X	X	X	X	X
Heterodon platyrhinos	X			X	X	
Coluber or *Masticophis*		X	X	X	X	X

Table 1.—*Continued.*

Taxon	Locality					
	FC	NP4	NC	CC	BB	KSC
Opheodrys aestivus		X		X		X
Opheodrys vernalis			X	X		
Cemophora coccinea			X	X		
Elaphe guttata		X	X	X		X
Elaphe obsoleta		X	X	X		X
Elaphe sp.					X	
Lampropeltis calligaster		X		X		X
Lampropeltis getulus		X	X	X	X	X
Lampropeltis triangulum		X	X	X	X	X
Pituophis melanoleucus		X				X
Lampropeltinae	X					
Agkistrodon contortrix	X	X	X			X
Crotalus horridus		X	X	X	X	
Crotalinae	X					

Family Viperidae
Subfamily Crotalinae
Agkistrodon contortrix (Linné)

Occurrence.—FC, NP4, NC, KSC.

Crotalus horridus Linné

Occurrence.—NP4, NC, CC, BB.

Large *Agkistrodon* are distinguished from *Crotalus* on the basis of a single fossa in a deep pit along each side of the cotyle in the former (Holman, 1981). A ridge extending from the accessory process ventrolaterally to the parapophysis defines the lateral border of the pit. *Crotalus* vertebrae usually have more than one fossa on a relatively flat surface on either side of the cotyle. Meylan (1982) reported that the number of fossae does not separate all *Agkistrodon* and *Crotalus* vertebrae, because some variation occurs along the vertebral column within individuals.

Richmond's report (in Guilday, 1962) of *C. adamanteus* from Natural Chimneys was based on a large *C. horridus* vertebra. The NSH is well within the range of variation for *C. horridus* and shorter than *C. adamanteus* of comparable size.

Annotated Faunal Lists

Complete specimen lists are available from the author on request. Table 1 permits comparison among herptiles listed for the six herpetofaunas. All identifications are by the author except as noted ([1]N. D. Richmond, [2]O. A. Peterson, [3]H. McGinnis, [4]J. E. Guilday, [5]G. H. Van Dam). An asterisk (*) indicates that the taxon no longer occurs near the locality. The designation "sp." is used when fossil and modern distributions indicate more than one member of the genus may be represented in material not assignable to species. Number of specimens is listed in parentheses following catalog number. Repository acronyms are CM—Carnegie Museum of Natural History and BC—Berry College.

Frankstown Cave

Location.—Blair County, Pennsylvania, latitude 40°25′N, longitude 78°22′W.
Accumulation.—Fissure fill.
Fauna.—Peterson (1926) listed six herptiles from Frankstown Cave. Richmond

(1964) restudied the collection and found 12 taxa, including four mis-identifi-
cations by Peterson. I have added or re-assigned eight taxa for a new total of 20
fossil herptiles from Frankstown Cave. Plethodontidae, *Storeria,* and *Crotalus* are
removed from the list.

Taxonomic changes by the author are as follows: Plethodontidae CM 11149 (1
caudal vertebra) assigned to *Ambystoma* sp., *Bufo* cf. *americanus* CM 11143 (2
ilia) to *Hyla chrysoscelis/versicolor, Bufo* cf. *americanus* CM 11143 (1 ilium-
juvenile) to *Bufo* sp., *Storeria* sp. CM 11051 (6 trunk vertebrae) to *Virginia
valeriae, Storeria* sp. CM 11051 (3 trunk vertebrae) to *Thamnophis brachystoma,
Storeria* sp. CM 11051 (8 trunk vertebrae) to Natricinae indeterminate, *Lampro-
peltis doliata* CM 11513 (9 trunk vertebrae-juvenile) to Lampropeltinae indeter-
minate, *Crotalus* sp. CM 11514 (1 trunk vertebra-juvenile) to Crotalinae inde-
terminate.

Notophthalmus viridescens[1]	CM 11150(8), 11151(2)
Ambystoma sp.	CM 11145(2), 11149(1)
Bufo americanus	CM 11133(3)
Bufo sp.	CM 11134(8)
Hyla chrysoscelis/versicolor	CM 11143(2)
Hyla crucifer	CM 11144(2)
Rana pipiens-group	CM 11147(1)
Rana sylvatica	CM 11140(3)
Rana sp.[2]	CM 11136–11139, 11141–11142, 11146, 11317 (38)
Clemmys insculpta[2]	CM 11065(2)
Nerodia sipedon	CM 11316(3)
*Thamnophis brachystoma	CM 41871(3)
Thamnophis sirtalis[2]	CM 11318(1), 31260(16)
Virginia valeriae	CM 11051(6)
Carphophis amoenus	CM 11351(2)
Diadophis punctatus	CM 11178(1)
Heterodon platyrhinos	CM 31262(1)
Lampropeltinae	CM 11513(9)
Agkistrodon contortrix	CM 11315(2)
Crotalinae	CM 11514(1)

Discussion. — No radiocarbon dates are available from this locality. It is con-
sidered of Wisconsinan Age (Kurtén and Anderson, 1980:76–77) and represen-
tatives of the eleven extinct mammal taxa reported from Frankstown Cave (Lun-
delius et al., 1983:333, 337, 338, 339, Table 16.6) are known to have survived
elsewhere at least until 12,000 yr BP (Mead and Meltzer, 1984:446, table 19.4).

The additions and changes to the herpetofaunal list represent a 62% increase
in taxa reported. This is a disharmonious unit due only to the restricted range of
Thamnophis brachystoma (Fig. 2), although all members inhabit some portion of
the Appalachian Plateau. The extant mammals of the local fauna (61% of mammal
taxa) are sympatric in the Valley and Ridge Province in West Virginia and Virginia
100 km south of the locality (Fig. 2). In part because screen-washing recovery
techniques were apparently not used at Frankstown (Holland, 1908; Peterson,
1926), this local fauna is not diverse enough to warrant detailed paleoenviron-
mental reconstruction, but climatic conditions similar to present are indicted by
the zoogeographic evidence. No other Late Wisconsinan–early Holocene local
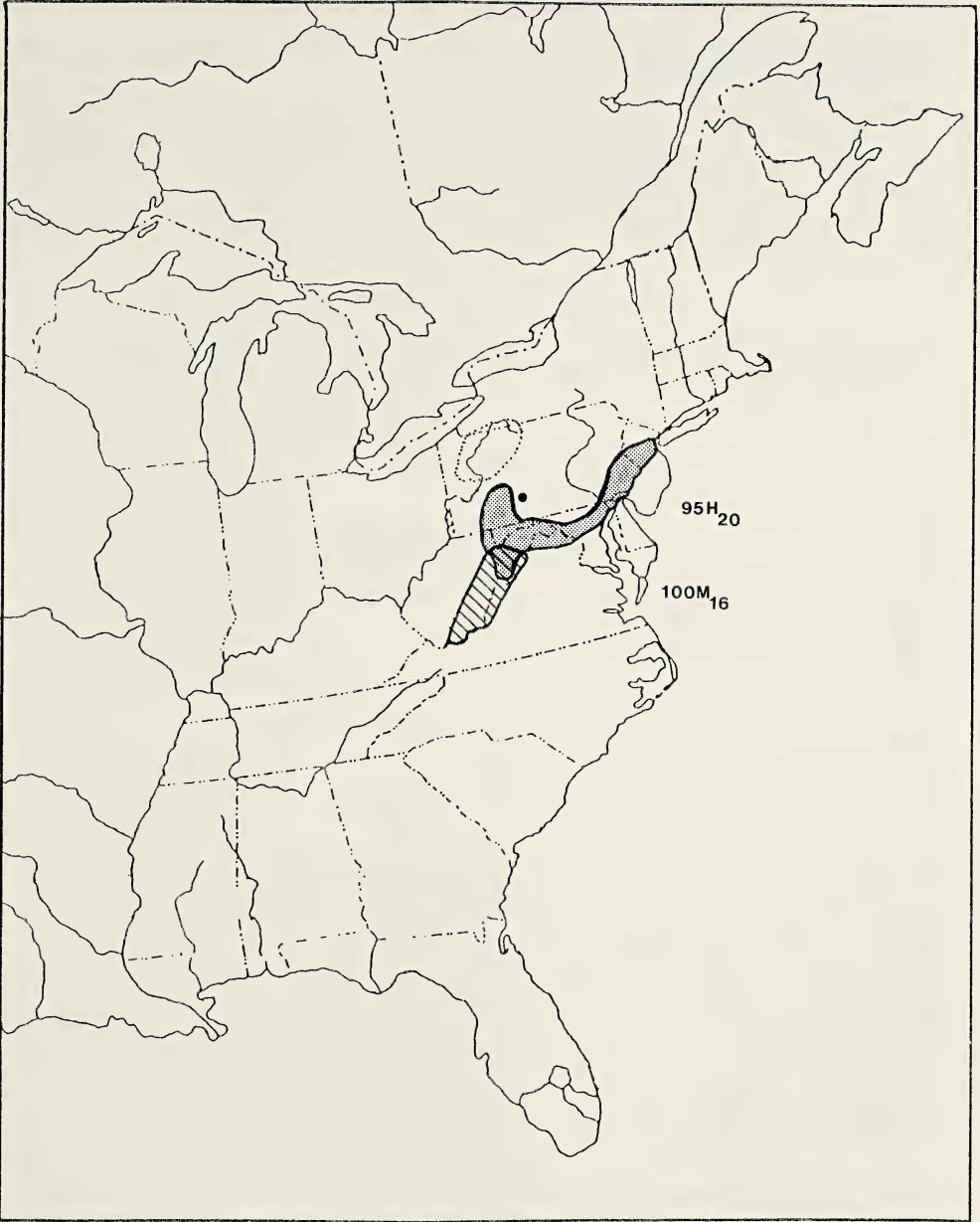
Fig. 2.—Sympatry map for Frankstown Cave local fauna. Dotted line encloses modern range of *Thamnophis brachystoma*. Closed circle indicates fossil locality. Shaded area is herptile sympatry, lined area is mammal sympatry. $95H_{20}$ = 95% of 20 extant herptile phena occur in sympatry area, $100M_{16}$ = 100% of 16 extant mammal phena occur in sympatry.

fauna from the central or southern Appalachian region shares this zoogeographic pattern of near-complete sympatry close to the fossil locality, suggesting that Frankstown Cave local fauna was deposited earlier, perhaps during a Wisconsinan interstadial episode.

New Paris No. 4

Location. — Bedford County, Pennsylvania, latitude 40°05′N, longitude 78°39′W.
Accumulation. — Fissure fill.

Fauna. — Richmond (in Guilday et al., 1964) reported 20 fossil herptile taxa
from New Paris No. 4. *Regina septemvittata* and *Storeria occipitomaculata* were
also identified by Richmond but not included in the published list. I assign *Pleth-
odon* cf. *glutinosus* to *Plethodon*-type. I have identified 14 additional taxa for a
total of 34 recognized forms (*B. a. copei* excluded, a subspecific determination
that I do not support).

	Unit A	Unit B
Notophthalmus viridescens[1]	CM 41928(11)	CM 41928(9)
Ambystoma maculatum-group (Tihen, 1958)	CM 41929(10)	CM 41929(1)
Ambystoma sp.[1]	CM 41930(11)	CM 41930(1)
Desmognathinae	CM 41931(6)	CM 41931(5)
Pseudotriton sp.	———	CM 41932(1)
Eurycea sp.[1]	CM 41933(19)	CM 41933(18)
Plethodon-type	CM 41934(203)	CM 41934(137)
Bufo americanus[1]	CM 7950(54)	CM 7952(69)
*Bufo americanus ?copei[1]	———	CM 7951(12)
Bufo woodhousei fowleri	———	CM 41935(1)
Hyla crucifer[1]	CM 12513(1), 12534(1)	CM 12533(1)
Rana ?clamitans	CM 41936(3)	———
Rana ?palustris	CM 41937(1)	CM 41937(2)
Rana pipiens-group[1]	CM 41938(22)	CM 41938(5)
Rana sylvatica[1]	CM 8017(53)	CM 8017(28)
Nerodia sipedon[1]	CM 41939(29)	CM 41939(2)
*?Regina septemvittata[1]	CM 41940(3)	———
Storeria dekayi	CM 41941(8)	CM 41941(4)
Storeria occipitomaculata[1]	CM 41942(7)	———
Thamnophis ?sauritus	CM 41943(13)	———
Thamnophis sirtalis[1]	CM 41944(3044)	CM 41944(2178)
Thamnophis sp.	CM 41945(1898)	CM 41945(167)
Virginia valeriae	CM 41946(23)	CM 41946(2)
Carphophis amoenus[1]	CM 41947(35)	———
Diadophis punctatus[1]	CM 41948(57)	CM 41948(3)
Coluber or *Masticophis*	CM 41949(17)	———
*Opheodrys aestivus	CM 41950(1)	———
Elaphe guttata	CM 41951(7)	———
Elaphe obsoleta[1]	CM 41952(151)	CM 41952(20)
*Lampropeltis calligaster	CM 41953(1)	———
*Lampropeltis getulus	CM 41954(46)	CM 41954(5)
Lampropeltis triangulum[1]	CM 41955(2)	———
*Pituophis melanoleucus[1]	CM 41956(3)	CM 41956(3)
Agkistrodon contortrix[1]	CM 41957(59)	CM 41957(6)
Crotalus horridus[1]	CM 41958(1289)	CM 41958(333)

Discussion. — Charcoal from Unit A, 1.5 m above the boundary with Unit B,
was dated at 11,300 ± 1000 yr BP (Y-727) (Guilday et al., 1964:132).

Table 2.—*Average stratigraphic depth (m) and current range limits of New Paris No. 4 fossil herptiles.*

Mean depth	Taxon	Current range (degrees north latitude)					
		40	45	50	55	60	65
2.6	*Coluber constrictor*	————	——				
2.7	*Nerodia sipedon*	————	—				
3.7	*Lampropeltis triangulum*	————	——				
3.8	*Lampropeltis getulus*	———					
3.9	*Regina septemvittata*	————	———				
4.1	*Pituophis melanoleucus*	—					
4.5	*Agkistrodon contortrix*	———					
4.7	*Thamnophis sauritus*	————					
4.8	*Crotalus horridus*	————					
5.0	*Elaphe guttata*	—					
5.0	*Storeria occipitomaculata*	————	————				
5.1	*Elaphe obsoleta*	————					
5.2	*Carphophis amoenus*	———					
5.2	*Virginia valeriae*	—					
5.2	*Diadophis punctatus*	————	——				
5.5	*Rana pipiens*		————	————	————	————	
5.5	*Rana sylvatica*		————	————	————	————	
5.6	*Ambystoma maculatum*-group		————	———			
5.6	*Rana clamitans*		————	————			
5.7	*Notophthalmus viridescens*		————	————			
5.8	*Eurycea* sp.		————	————			
5.8	*Plethodon*-type		————	————			
5.9	Desmognathinae		————	———			
6.1	*Thamnophis sirtalis*		————	————	———		
6.3	*Storeria dekayi*		————				
6.6	*Bufo americanus*		————	————	————		
7.0	*Hyla crucifer*		————	————	———		
7.2	*Rana palustris*		————	————			

The newly identified animals are ecologically compatible with the rest of the herpetofauna, which is now widely distributed in eastern North America. Five snake species now extirpated from the locality are sympatric in the southern Appalachians. *Regina septemvittata, Opheodrys aestivus, Lampropeltis calligaster,* and *L. getulus* range further north in the Coastal Plain-Piedmont and/or Appalachian Plateau than in the Valley and Ridge Province, indicating topographic control on distributional limits through the Holocene. Other factors have caused the southerly range retraction of *Pituophis melanoleucus,* which exhibits the opposite pattern—northernmost regional distribution in the Valley and Ridge Province 100 km south of New Paris. It remains unclear why the ranges of these five species no longer include the New Paris area.

When arrayed by mean depth in the deposit and maximum current northern range limits, the mammalian component above 5.9 m in the New Paris No. 4 deposit is relatively temperate (50°N latitude or less) in character, below 5.9 m boreal (Guilday et al., 1964:178, table 390. Treating the herptiles in the same manner for comparison (Table 2), the change is similar although less pronounced and higher in the section. Above 5.5 m only two of 15 taxa range north beyond 50°, below 5.5 m 11 of 13 have north limits at or beyond 50°. Ten of 14 mammal taxa found in the lowest meter of the section are present today at Great Whale River, Québec, at the boundary of the Arctic and Hudsonian life zones (Guilday et al., 1964:179). Only two amphibians from the lowest meter, *Rana sylvatica* and *Bufo americanus,* occur with these mammals at Great Whale River. *Rana*

89M₃₅

100H₃₂
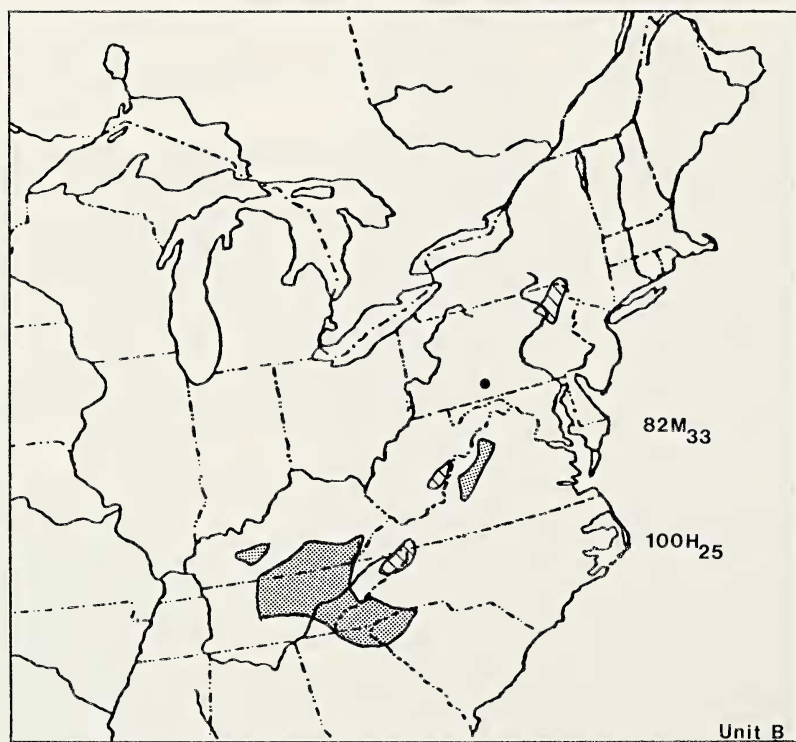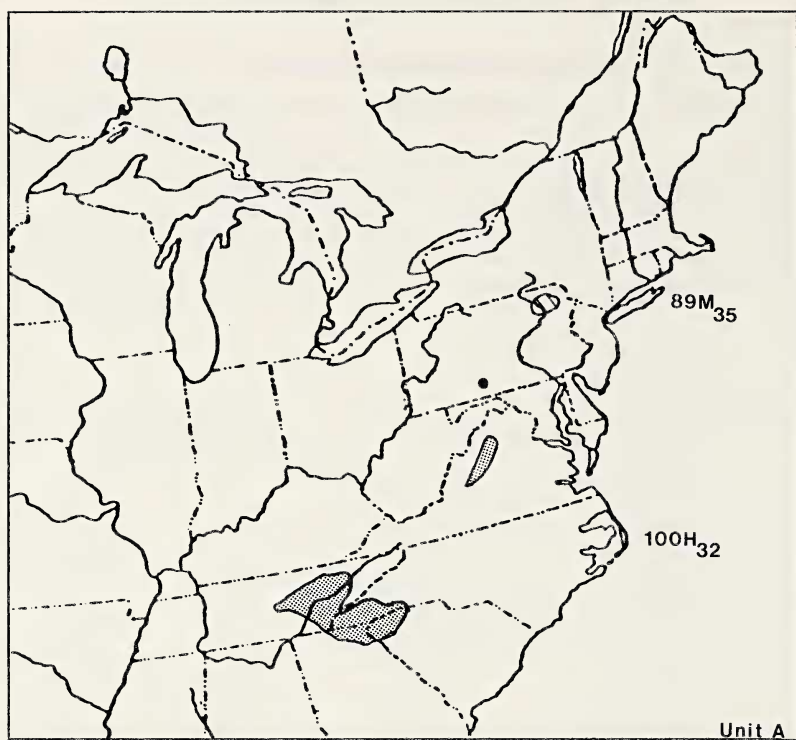
Unit A

82M₃₃

100H₂₅

Unit B

Fig. 3.—Sympatry maps for New Paris No. 4 local faunules. Symbols as in Fig. 2.

pipiens and *Thamnophis sirtalis* range almost as far north, but the other three herptiles of the lowest meter at New Paris do not have northern limits within the boreal zone. All seven have widespread distributions that also include the New Paris locality today, but five of the 14 mammals are not resident in the New Paris area, emphasizing the zoogeographic anomaly between vertebrate classes.

Unit A vertebrates comprise a temperate fauna with a partial mammalian sympatry (31 of 35 extant taxa—89%) in the Pocono Mountains of northeastern Pennsylvania and two sympatric areas for all 32 herptiles in the Virginia Blue Ridge Mountains and at the southern end of the Appalachians in North and South Carolina, Tennessee, and Georgia (Fig. 3A). The partial sympatry for Unit B mammals (Fig. 3B) tells a conflicting story. Consisting of three isolated segments spread through the central and southern Appalachians, only 82% (27 of 33) extant taxa are included. Of Unit B mammals, 15% are boreal, 3% steppe. This is a classic disharmonious faunule, once again contrasting sharply with co-occurring herptiles.

The bird component of New Paris No. 4 is small. Of seven species, only one (*Pedioecetes phasianellus*) has a boreal distribution that does not reach south-central Pennsylvania now.

Guilday et al. (1964:188) assert that the boreal biota of New Paris No. 4 does not support the view (fide Braun, 1950) that the central Appalachians provided a refugium for temperate plants and animals during the late glacial (ca. 15,000–10,000 yr BP). Completed study of the New Paris No. 4 herptiles compromises this statement, as all 32 herptile taxa now live at or further south than New Paris.

All New Paris No. 4 herptiles are small enough to have been prey items for raptorial birds or other predators. Many of the taxa live in or near cave mouths and fissures. It is difficult to determine if herptiles in a fossil accumulation were contributed through predation, accidental falls, or attrition of residents at the accumulation site. Large predatory herptiles, such as the rattlesnakes and garter snakes that dominate the New Paris herpetofauna, very likely denned in the New Paris sinkholes and accumulated there either by attrition over many seasons or during one or more short-term environmental crises. It has not been determined if such hibernaculum mortality types can be distinguished, especially in sinkholes where rate of sedimentation is not readily discerned.

Natural Chimneys

Location.—Augusta County, Virginia, latitude 38°22′N, longitude 78°05′W.
Accumulation.—Raptor roost.
Fauna.—The Natural Chimneys herpetofauna was first reported by Richmond (in Guilday, 1962) with 17 taxa, of which I reject three (*Hyla* sp. CM 7609 [1 ilium] assigned to *Scaphiopus holbrooki, Masticophis flagellum* CM 7596 [1 trunk vertebra] to *Coluber* or *Masticophis, Crotalus* cf. *adamanteus* CM 7614 [1 trunk vertebra] to *Crotalus horridus*). I have identified 27 additional taxa (including 16 species from Richmond's genera) for a total of 41 herptiles. This expansion results from new material collected in 1977 as well as re-examination of the original collection.

Notophthalmus viridescens[1]	CM 7611(10)
Ambystoma maculatum-group	CM 7612(14)
Ambystoma opacum-group (Tihen, 1958)	CM 41903(2)

*Ambystoma tigrinum	CM 41904(5)
Desmognathinae	CM 7610(2)
Gyrinophilus porphyriticus	CM 41905(11)
Pseudotriton sp.	CM 41906(51)
Eurycea sp.	CM 41907(25)
Plethodon-type	CM 41908(349)
Scaphiopus holbrooki[1]	CM 7606(8), 7609(1)
Bufo americanus	CM 7605(60)
Bufo woodhousei fowleri	CM 41909(9)
Rana catesbeiana[1]	CM 7608(3)
Rana clamitans	CM 41910(6)
Rana ?palustris[1]	CM 7607(5)
*Rana pipiens-group[1]	CM 41911(130)
Rana sylvatica	CM 41912(22)
Chelydra serpentina[1]	CM 7589(1)
Terrapene carolina[1]	CM 41915(4)
Sceloporus undulatus[1]	CM 7603(9)
*Scincella lateralis	CM 41916(1)
*Nerodia ?erythrogaster	CM 41917(1)
Nerodia sipedon	CM 7592(20)
?Regina septemvittata	CM 41918(2)
Storeria dekayi	CM 41919(1)
Storeria occipitomaculata	CM 41920(9)
Thamnophis sirtalis[1]	CM 7591(346)
Thamnophis sp.	CM 41921(151)
*Virginia striatula	CM 41922(1)
Virginia valeriae	CM 41923(10)
Carphophis amoenus[1]	CM 7602(5)
Diadophis punctatus[1]	CM 7600(27)
Coluber or Masticophis	CM 7590(57), 7594(1), 7596(1)
Opheodrys vernalis	CM 41924(3)
Cemophora coccinea	CM 41925(1)
Elaphe guttata[1]	CM 7595(15)
Elaphe obsoleta	CM 41926(4)
Lampropeltis getulus	CM 7597(7)
Lampropeltis triangulum[1]	CM 7593(161)
Agkistrodon contortrix[1]	CM 41927(7)
Crotalus horridus[1]	CM 7601(88), 7614(1)

Discussion. —Guilday (1962) considered the Natural Chimneys sample hetero-chronic, having accumulated over thousands of years. If this was the case, the composition of the local fauna did not change during the interval of deposition. That is, no disharmonious elements (beyond the boreal + temperate admixture, discovered to be synchronous since Guilday's 1962 paper) are recorded. Of the four extinct mammals from Natural Chimneys, two are large subspecies of living forms (*Tamiasciurus hudsonicus tenuidens* Guilday et al., 1964 and *Eptesicus fuscus grandis* Guilday, 1967) and two became extinct at the end of the Wisconsinan or early in the Holocene (*Castoroides ohioensis* 10,230 ± 150 yr BP, *Mylohyus nasutus* 9410 ± 155 yr BP; Mead and Meltzer, 1984:446, Table 19.4). Thus, Guilday's biochronologic assessment of earliest Holocene age for the Nat-

ural Chimneys local fauna is a minimum date, according to radiometric dating of congeneric material from other localities.

The most important change in the herpetofaunal list is the rejection of *Masticophis flagellum* and *Crotalus adamanteus*. The Natural Chimneys herpetofauna has been considered a southern association, in strong contrast with the boreal and temperate mammal and bird component (Guilday, 1962; Lundelius et al., 1983). In the corrected list, all herptiles reach the latitude of Natural Chimneys, but five taxa (*Rana pipiens*-group, *Ambystoma tigrinum, Scincella lateralis, Nerodia erythrogaster,* and *Virgina striatula*) no longer inhabit the Valley and Ridge Province in Virginia. Of the five, *Rana pipiens*-group distribution surrounds the area on all sides, while the others occur to the east in the Piedmont (*S. lateralis* and *V. striatula*) and Coastal Plain (*A. tigrinum* and *N. erythrogaster*) or to the west on the Appalachian Plateau (*S. lateralis*) and in the Central Lowlands of the Midwest (*A. tigrinum* and *N. erythrogaster*). All five are widely distributed in the Carolinian Biotic Province, but not closely linked with the Austroriparian Province as are *M. flagellum* and *C. adamanteus*.

The herptile partial sympatry (Fig. 4) is located in the same southern Appalachian area as those of New Paris No. 4. Two of the three members of the fossil sample not present in the sympatry are now excluded from the Valley and Ridge Province, although their nearest range limit is within 50 km of the sympatry. *Opheodrys vernalis* currently occupies the fossil locality but not the sympatry area. A southern shift of a portion of the herptile association after Natural Chimneys time is indicated, although not the more extreme shift previously assumed, i.e., no truly austroriparian element is involved.

The mammal partial sympatry (Fig. 4), like that of New Paris No. 4, is located in northeastern Pennsylvania, but with a greater number of taxa present from Natural Chimneys (47 of 50 extant taxa from NC, 27 of 33 from NP4 Unit B, 31 of 35 from NP4 Unit A). The zoogeography of the Natural Chimneys local fauna indicates it is younger than New Paris No. 4 (Guilday, 1962).

It has been stated that the herptiles of Natural Chimneys disagree with the mammals (Lundelius et al., 1983) in a paleoenvironmental sense. A literal interpretation of decreased annual temperatures (or summer extremes) based on mammals and increased annual temperatures (or length of warm season) based on herptiles is indeed contradictory, but within the paradigm of climatic equability. All vertebrate classes from Natural Chimneys indicate climatic conditions that allowed species now occupying widely disparate habitats to exist in sufficient proximity for their remains to be preserved at a single locality.

Clark's Cave

Location.—Bath County, Virginia, latitude 38°05'10"N, longitude 79°39'25"W.
Accumulation.—Raptor roost.
Fauna.—The Clark's Cave herpetofauna was partially reported in Guilday et al. (1977). Their list includes 14 taxa, ranging in rank from species to family. I have added 33 identifications (all from higher taxa previously listed) for a total of 42 herptile taxa.

Notophthalmus viridescens	CM 41872(24)
Ambystoma maculatum-group	CM 41873(148)
Ambystoma opacum-group	CM 41874(1)
Ambystoma sp.[3]	CM 29692(122)

Fig. 4.—Sympatry map for Natural Chimneys local fauna. Symbols as in Fig. 2.

Desmognathinae	CM 41875(94)
Gyrinophilus porphyriticus	CM 41876(2)
Pseudotriton sp.	CM 41877(8)
Eurycea sp.	CM 41878(20)
Plethodon-type	CM 41879(256)
Scaphiopus holbrooki	CM 41880(1)

Bufo americanus	CM 29582(273)
Bufo woodhousei fowleri	CM 41881(7)
Hyla crucifer[3]	CM 29581(37)
Rana catesbeiana[3]	CM 29574(7)
Rana clamitans[3]	CM 29575(3)
Rana palustris[3]	CM 29578(40)
Rana pipiens-group[3]	CM 29577(35)
Rana sylvatica[3]	CM 29579(83)
*Graptemys geographica	CM 29695(1)
Sceloporus undulatus[4]	CM 29584(13)
Eumeces ?laticeps[4]	CM 29585(2)
Nerodia sipedon	CM 41882(37)
?Regina septemvittata	CM 41883(1)
Storeria dekayi	CM 41884(86)
Storeria occipitomaculata	CM 41885(61)
Thamnophis ?sauritus	CM 41886(9)
Thamnophis sirtalis	CM 41887(366)
*Virginia striatula	CM 41889(19)
Virginia valeriae	CM 41890(16)
Carphophis amoenus	CM 41891(49)
Diadophis punctatus	CM 41892(124)
Heterodon platyrhinos	CM 41893(3)
Coluber or *Masticophis*	CM 41894(12)
Opheodrys aestivus	CM 41895(47)
Opheodrys vernalis	CM 41896(6)
*Cemophora coccinea	CM 41897(6)
Elaphe guttata	CM 41898(9)
Elaphe obsoleta	CM 41899(10)
Lampropeltis calligaster	CM 41900(4)
Lampropeltis getulus	CM 41901(9)
Lampropeltis triangulum	CM 41902(78)
Crotalus horridus	CM 29694(5)

Discussion.—The mammals of Clark's Cave are very similar to those of New Paris No. 4, indicating an age assessment for the Clark's Cave local fauna of ca. 11,000 yr BP (Guilday et al., 1977). The herpetofauna is more similar to that of Natural Chimneys than New Paris No. 4, but the difference may not be significant, because diversity is less in the New Paris sample than in the other two.

Four reptiles (*Graptemys geographica, Virginia striatula, Cemophora coccinea,* and *Lampropeltis calligaster*) plus the *Rana pipiens*-group frogs do not presently occur at the locality. The average distance by which they are removed from Clark's Cave is 90 km and the most distant herptile, the leopard frog, is no more than 125 km away. This minor disjunction requires little invocation of climatic change. Periodic fluctuations of range limits in response to various short-term edaphic or biotic perturbations (as yet undiscovered from the fossil or climatic proxy records) or even insufficient documentation of true ranges may explain the extirpation. The Clark's Cave fossil herptiles have a partial sympatry in the Great Smoky Mountains (Fig. 5). Two snakes do not reach this sympatry; *Opheodrys vernalis* 250 km to the north and *Virginia striatula* 100 km to the south, in the same pattern of disjunction as for Natural Chimneys. This appears to be a small-scale version of climatic equability, with taxa from both north and south indicating

Fig. 5.—Sympatry map for Clark's Cave local fauna. Symbols as in Fig. 2.

reduced climatic extremes. However, with only three snake species involved be-
tween two localities, I consider this not a case of climatic equability, as the taxa
in question do co-exist elsewhere within their ranges. It is an example of indi-
vidualistic response to local microhabitat availability. The partial sympatry area
for Natural Chimneys and Clark's Cave plus one of the complete sympatry areas
for New Paris No. 4 includes the Great Smoky Mountains. This likely reflects

surviving habitat diversity in that area rather than a single set of ecologic conditions suitable for all taxa, as a consequence of unit-fauna retreat from western Virginia and Pennsylvania.

Fifty-two percent of the Clark's Cave fossil mammal taxa do not presently occur in the central Appalachians, live only at higher elevations in the region, or are of sizes indicating boreal rather than temperate populations (Guilday et al., 1977). Seven percent of the avifauna does not presently spend any part of the year in the central Appalachians (Guilday et al., 1977). Why can every herptile of the local fauna still be found within 125 km after 11,000 years of climatic and biotic change that has driven out several birds and many mammals? Climatic equability is not the best answer, as northern herptiles were apparently not present and only a slight southward shift of those represented as fossils is evident.

Baker Bluff Cave

Location. — Sullivan County, Tennessee, latitude 36°27'30"N, longitude 82°28'00"W.

Accumulation. — Raptor roost.

Fauna. — Only minor changes to Van Dam's (1978) faunal list are made in this review. 22 taxa are recorded from the mid-levels of Baker Bluff Cave, the interval comparable to the time of deposition for the other herpetofaunas of this study.

Taxonomic changes from Van Dam (1978) for all levels are as follows: *Ambystoma opacum* altered to *A. opacum*-group, *Desmognathus* sp. to Desmognathinae, *Hyla* sp. CM 29802 (1 left ilium) assigned to *Bufo* sp. juvenile.

mid-levels (5–7 ft) only

Cryptobranchus alleganiensis[5]	CM 29776–777(42)
Necturus maculosus[5]	CM 29770–771(8)
Ambystoma maculatum-group[5]	CM 29759–760(7)
Ambystoma opacum-group[5]	CM 29755–756(6)
Ambystoma sp.[5]	CM 29763–764(14)
Desmognathinae[5]	CM 29782–783(176)
Bufo americanus[5]	CM 29788–789(30)
Bufo woodhousei fowleri[5]	CM 29795(6)
Rana sylvatica[5]	CM 29805–806(14)
Rana sp.[5]	CM 29811–812(3)
Eumeces fasciatus[5]	CM 29817(1)
Nerodia sipedon[5]	CM 29852(3)
Nerodia sp.[5]	CM 29853(1)
Thamnophis sirtalis[5]	CM 29859–860(3)
Thamnophis sp.[5]	CM 29863–864(5)
Diadophis punctatus[5]	CM 29830(6)
Heterodon platyrhinos[5]	CM 29825–826(2)
Coluber or *Masticophis*[5]	CM 29834–835(10)
?*Elaphe* sp.[5]	CM 29849(3)
Lampropeltis getulus[5]	CM 29846(6)
Lampropeltis triangulum[5]	CM 29840–841(16)
Crotalus horridus[5]	CM 29820–821(36)

Discussion. — This stratified local fauna ranges in age from 19,100 ± 100 yr BP to 200 yr BP (Guilday et al., 1978:53). The mid-levels date from approximately
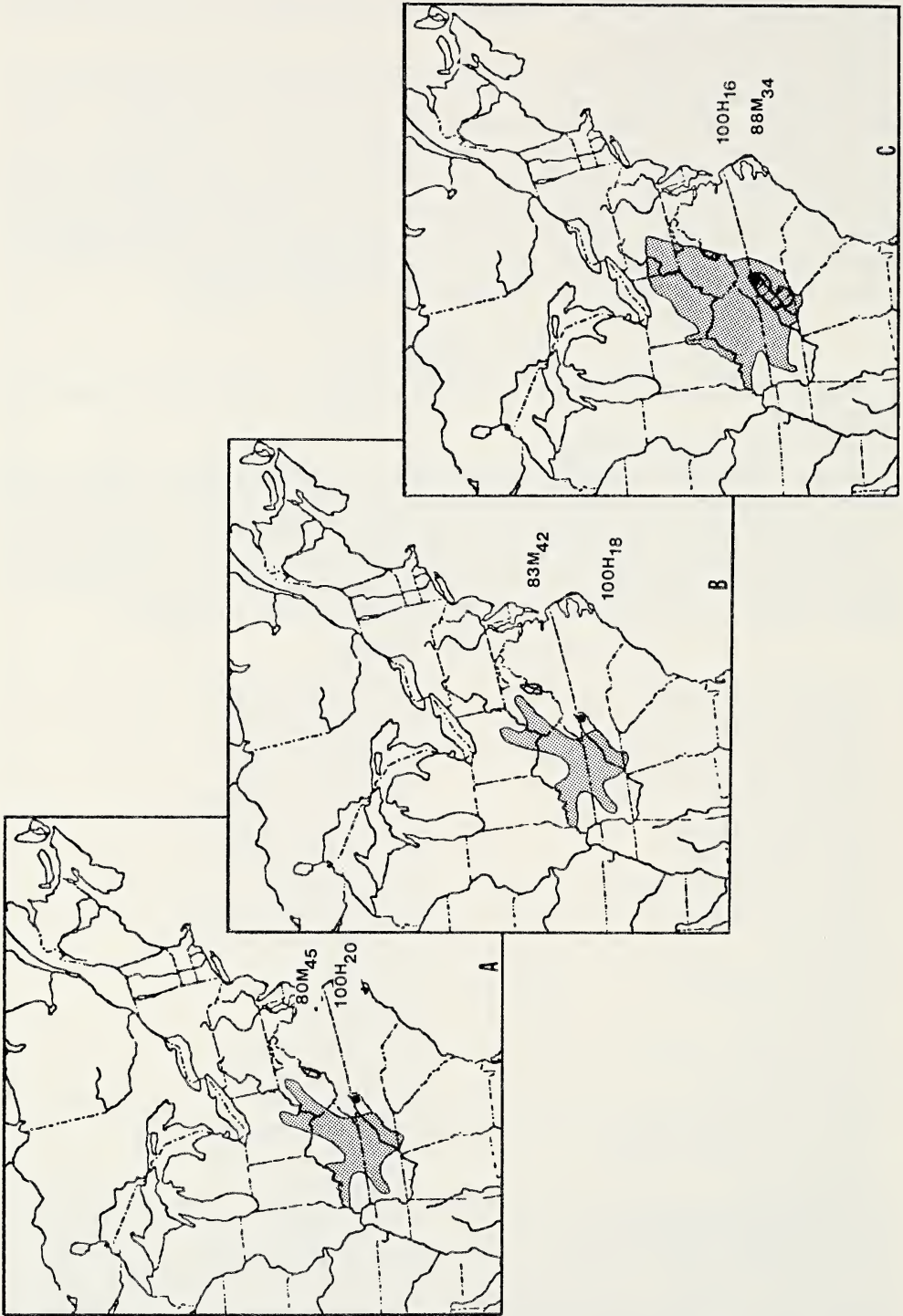
10,560 to 11,640 yr BP (Guilday et al., 1978:53). Seventy-two percent of the Baker Bluff herptile taxa (18 of 25) are recorded in the mid-levels.

All but one of the herptiles presently live in the immediate area. *Lampropeltis getulus* has its nearest range limit only 65 km east of the locality. All the taxa are widely sympatric through the Appalachian Plateau west of Baker Bluff (Fig. 6B). A slight increase in effective precipitation compared to the present condition is indicated by this zoogeographic shift.

Van Dam (1978) asserted that no discernible trends occur in the herpetofauna that reflect ecologic or climatic change through the past 20,000 years in northeastern Tennessee. Sympatry maps for the three faunules (Fig. 6A–C) support Van Dam's conclusions. The mammal partial sympatry is located in the same area as the middle of the three areas for New Paris No. 4 Unit B (Fig. 3B). Although the sympatry area remains in the same location, the percentage of Baker Bluff mammal taxa participating decreases from ca. 20,000 to 200 yr BP.

Kingston Saltpeter Cave

Location. — Bartow County, Georgia, latitude 34°12′18″N, longitude 84°54′55″W.
Accumulation. — Cave/?raptor roost.

Fauna. — Preliminary reports on Kingston Saltpeter Cave (Blair et al., 1981; Sneed, 1981) include partial lists of vertebrates recovered. The 43 herptile taxa reported here comprise the first comprehensive listing from the local fauna. *Storeria* sp. refers to damaged vertebrae that may represent *S. dekayi*, *S. occipitomaculata,* or even *Virginia* spp. A complete study of the paleontology and history of the cave is underway.

Notophthalmus viridescens	BC 35(2)
Ambystoma maculatum-group	BC 36(46)
Ambystoma opacum-group	BC 37(80)
Ambystoma tigrinum	BC 38(26)
Desmognathinae	BC 40(33)
Pseudotriton ruber	BC 43(7)
Eurycea sp.	BC 42(10)
Plethodon-type	BC 41(302)
Scaphiopus holbrooki	BC 44(19)
Bufo americanus	BC 45(33)
Bufo woodhuosei fowleri	BC 46(4)
Hyla crucifer	BC 48(1)
Gastrophryne carolinensis	BC 49(15)
Rana catesbeiana	BC 50(21)
Rana clamitans	BC 51(2)
Rana pipiens-group	BC 52(72)
Rana sp.	BC 53(47)
Kinosternidae	BC 54(2)
Chrysemys picta	BC 55(8)
?Clemmys insculpta or *?Pseudemys concinna*	BC 57(1)

←

Fig. 6.—Symptry maps for Baker Bluff Cave local faunules. A—upper levels (200 yr BP–10,560 rcybp), B—mid levels (10,560–11,560 rcybp), C—lower levels (11,640–19,100 rcybp). Symbols as in Fig. 2.

Pseudemys ?*concinna* or *Pseud-emys* ?*scripta*	BC 58(1)
Terrapene carolina	BC 56(40)
Anolis carolinensis	BC 59(11)
Sceloporus undulatus	BC 60(6)
Scincella lateralis	BC 61(1)
Nerodia sipedon	BC 62(70)
Storeria dekayi	BC 63(6)
?*Storeria* sp.	BC 64(31)
Thamnophis ?*sauritus*	BC 65(41)
Thamnophis sirtalis	BC 66(156)
Virginia striatula	BC 68(5)
Virginia valeriae	BC 69(2)
Carphophis amoenus	BC 70(1)
Diadophis punctatus	BC 71(7)
Coluber or *Masticophis*	BC 72(21)
Opheodrys ?*aestivus*	BC 73(3)
Elaphe guttata	BC 74(23)
Elaphe obsoleta	BC 75(32)
Lampropeltis calligaster	BC 76(16)
Lampropeltis getulus	BC 77(10)
Lampropeltis triangulum	BC 78(15)
Pituophis melanoleucus	BC 79(15)
Agkistrodon contortrix	BC 80(10)

Discussion.—Bone collagen from this local fauna was dated at $10,300 \pm 130$ yr BP (Beta 12771). The herpetofauna is sympatric and currently occupies much of northern Alabama and the northwestern corner of Georgia near the fossil locality (Fig. 7). Climatic requirements for southern Appalachian herptiles were nearly equivalent to modern conditions at the close of the Wisconsinan Age.

The fossil accumulation was recovered from cave earth matrix dissimilar to the surficial regolith (fissure fills) in which nearby Ladds Quarry local fauna was found (J. A. Holman, personal communication, July 1985). The two herpetofaunas are similar except for five extralimital records and *Geochelone crassiscutata,* an extinct giant land tortoise, at Ladds (Holman, 1985a). As the local faunas are nearly contemporaneous (Ladds dates: $10,940 \pm 210$ and $10,290 \pm 100$ yr BP; Holman, 1985b), taphonomic factors as yet undiscovered must be responsible for the faunal differences.

The Kingston fossil mammals are characteristic of high elevation habitats of the central Appalachians (Fig. 7), with only one boreal (*Phenacomys intermedius*) and one southern (*Panthera onca*) species (Fay and Wilson, in preparation). A similar, disharmonious association has been reported from Ladds Quarry (Ray, 1967; Lundelius et al., 1983).

DISCUSSION

Why are temperate herptiles found in association with boreal + temperate birds and mammals in Appalachian local faunas? The lack of boreal herptiles in the Late Wisconsinan fossil record may be due to the nature of potential migrants forced out of northeastern North America by glacial ice. There are only two "boreal" herptiles (defined here as occurring mostly within the area of northern hardwood and coniferous forests) that range east of the Great Lakes and north of
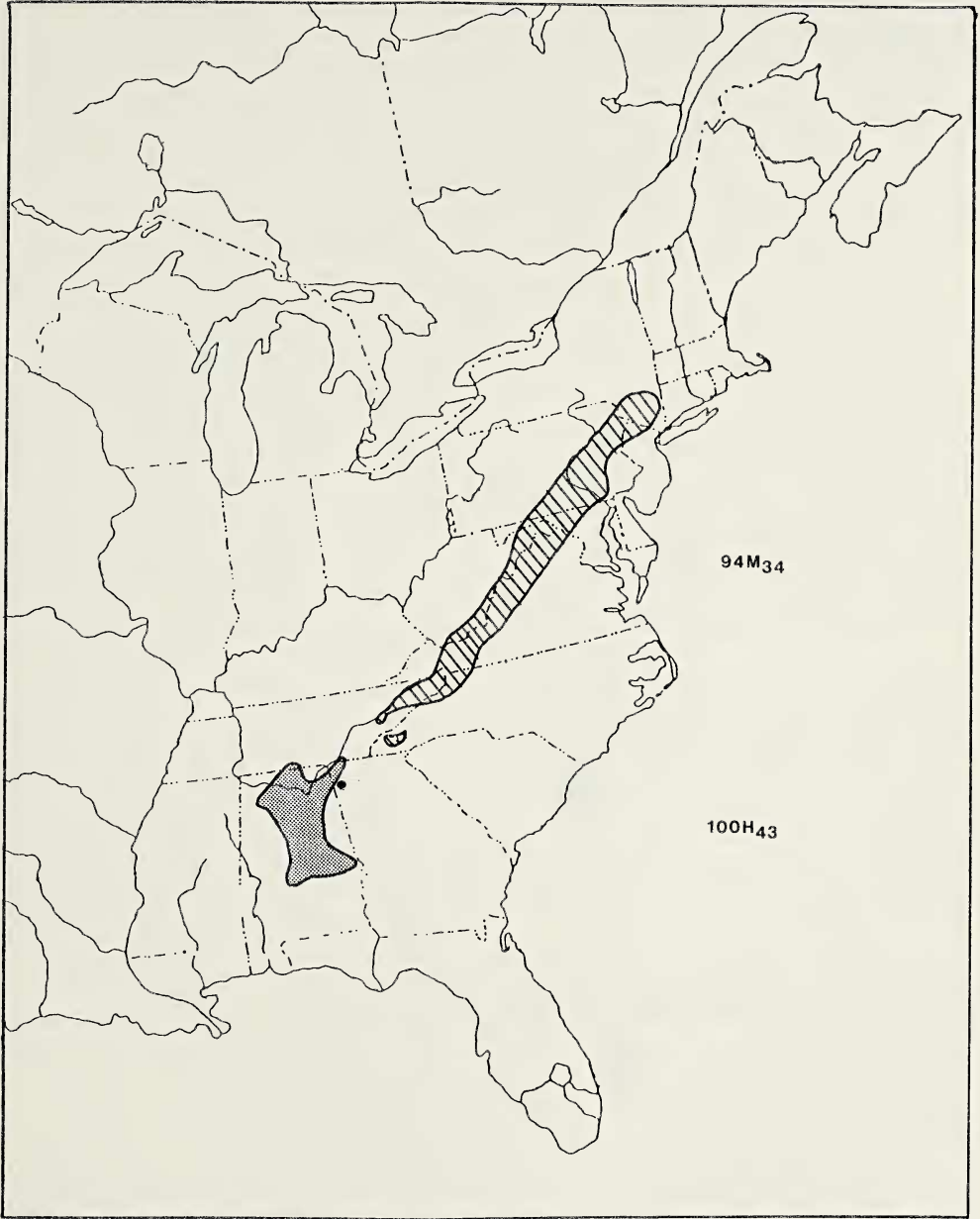
Fig. 7.—Sympatry map for Kingston Saltpeter Cave local fauna. Symbols as in Fig. 2.

central Pennsylvania (i.e. north of the southern and central Appalachian region of this study) (Fig. 8). *Ambystoma laterale* and *Rana septentrionalis* are difficult to distinguish osteologically from more widely distributed congeners and only *A. laterale* has been reported as fossils (Fay, 1984*a*). The two species may not appear in the central Appalachian fossil record because (1) They did not evolve before the Holocene, (2) Wisconsinan ice displaced them to another region (e.g., Appalachian Plateau or exposed continental shelf) with a more poorly known fossil
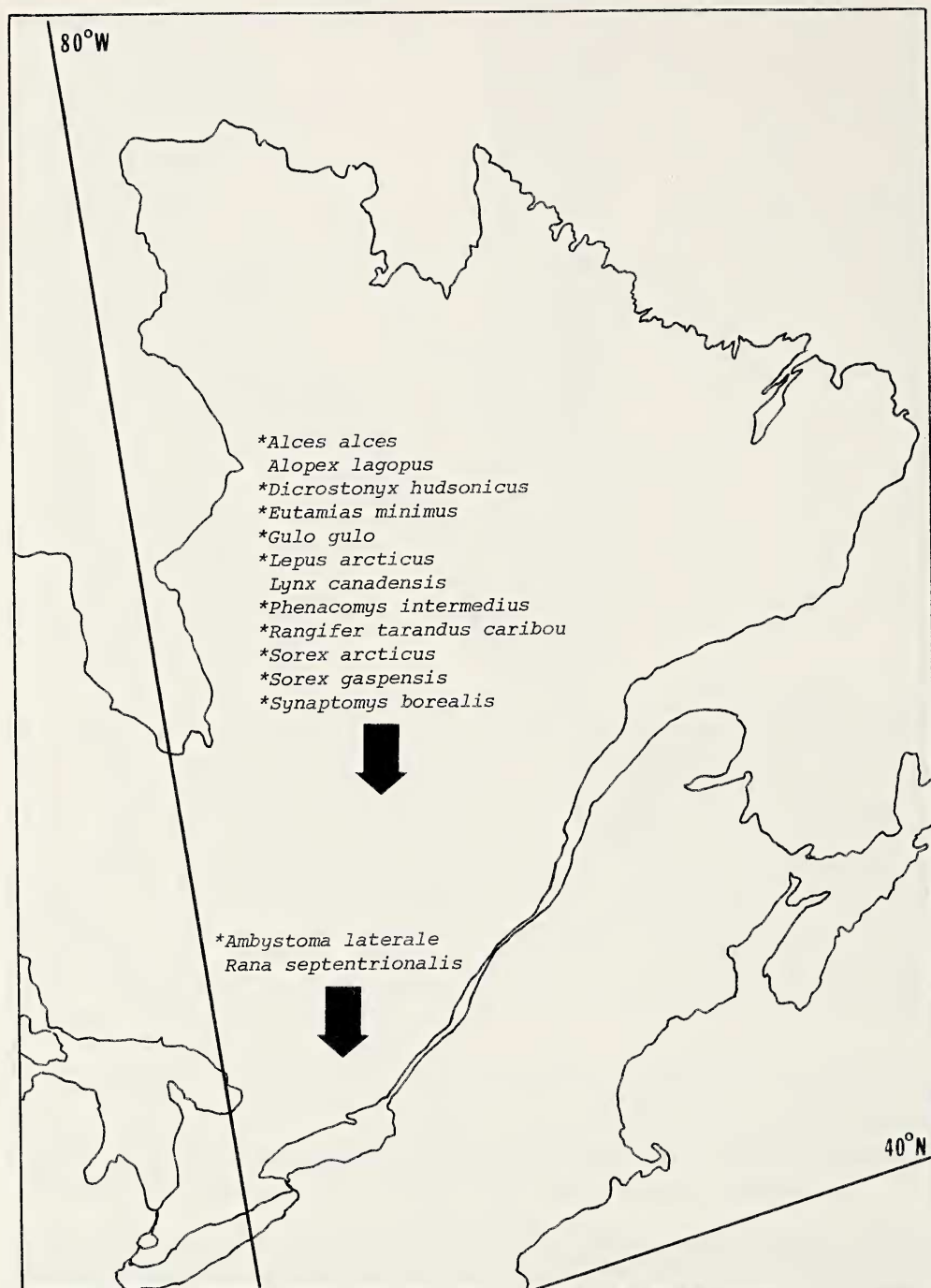
Fig. 8.— Mammals and amphibians with eastern North American range limits presently north of 42°N. Asterisks denote species with Late Wisconsinan–early Holocene fossil record in the Appalachian region.

record, or (3) they were present in the central Appalachians at very low densities or are not distinguishable from congeneric fossils (Fay, 1986). Until identification criteria are devised, these scenarios cannot be tested. Twelve mammals from the same northeastern region, all with fossil records (ten from within that region), do not now range further south in the Appalachians than central Pennsylvania (Fig. 8) (Fay, 1984b, 1986). Many herptile taxa that are partially sympatric in the north with these "boreal" mammals are also widely distributed in more temperate regions, obscuring any boreal vs. temperate indications that might contribute to paleoenvironmental reconstructions. Additional studies of clinal variation within herptile taxa will address this problem.

Extirpated species from these fossil localities may have been excluded by climatic or biotic changes since latest Wisconsinan time. The environment of the central Appalachians has seemingly become unsuitable for these animals, or the method by which they were added to the fossil accumulations no longer operates. Older herpetofaunas of the region also contain extirpated taxa. Three Irvingtonian local faunas (Cumberland Cave, Maryland [Holman, 1977a]; Trout Cave-Lower Level, West Virginia [Holman, 1982]; and Hanover Quarry Fissure, Adams County, Pennsylvania [Fay, in preparation]) include herptiles that have retracted their range limits to the north, west, or east outside the central Appalachians. This suggests a gradual shrinking of species distribution through the Neogene, as one species (*Elaphe vulpina*) is also known from the late-glacial Wisconsinan of Georgia (Holman, 1985a), Pliocene of Idaho (Holman, 1968), and several other now extralimital fossil localities (see Holman, 1979, 1981).

Some eastern North American endemic herptiles, such as *Clemmys muhlenbergi, Eumeces a. anthracinus, Pseudotriton montanus,* and *Scaphiopus holbrooki,* have discontinuous Appalachian ranges. Two possibilities would explain both their discontinuous ranges and the apparent extirpation of some of these and other taxa since the Late Wisconsinan. Physical and biological factors of central Appalachian habitats may have changed beyond the tolerances of these animals, or current distributions may be incompletely known and the animals actually occupy the entire region in suitable microhabitats. The latter is quite likely for *Clemmys muhlenbergi* (Bury, 1979) and perhaps for *Rana pipiens* (McCoy, 1982).

Zoogeography of the local faunas can be employed to illustrate tentative paleoenvironmental reconstructions (as mentioned previously, details of individual species range changes and modern autecology will strengthen future attempts to define the partial analog). As expected, areas of greatest partial sympatry for mammals and herptiles of all six local faunas (Fig. 2–7) are within the Appalachian Mountains and/or Plateau physiographic provinces. Herptiles "missing" from the sympatries are found within several hundred kilometers in similar or identical habitats. Most extralimital mammals, on the other hand, now range no closer to the sympatries than eastern Canada and many are removed over 1000 km to the west or northwest. Birds of these local faunas are not included on the maps because of low species diversity for most samples. They do, however, follow the mammalian pattern of regional + extralimital ("boreal") habitat distribution.

Mammal partial sympatries are situated further north than both herptile sympatry and fossil locality for all but the three oldest faunules illustrated (Frankstown Cave, Fig. 2; New Paris No. 4, Unit B, Fig. 3B; Baker Bluff Cave lower levels, Fig. 6C). Frankstown and Baker Bluff lower levels are the only faunules with overlapping herptile-mammal sympatries, and the latter is the only instance in which maximum partial sympatry includes the fossil locality. This pattern implies

that environmental conditions prior to ca. 12,000 yr BP were more similar to the present than latest Wisconsinan environments.

Herptile sympatries for the Pennsylvania and Virginia faunules (excluding the pre-latest Wisconsinan Frankstown Cave and New Paris No. 4, Unit B) are located 150 to 750 km south of the fossil localities (Fig. 3A, 4, 5), while sympatries for the Tennessee and Georgia faunules are at the same latitude and within 50 km of the localities (Fig. 6B, 7). For the Pennsylvania and Virginia faunules, herptiles appear to represent the environments of the Great Smoky Mountains near the south end of the Appalachian region, while mammals (extra-regionals excluded) are characteristic of Pocono Mountain environments at the north end of the central Appalachians. For Baker Bluff mid levels (Fig. 6B), mammals are characteristic of central Appalachian environments while herptiles appear to be shifted west onto the Appalachian Plateau (due to small sample size). Kingston exhibits a mammal pattern unique among these faunas, spanning the entire central Appalachians (Fig. 7). It is also the only local fauna of this study with species now occurring far to the north (*Phenacomys intermedius*) and south (*Panthera onca*) (Fay and Wilson, in preparation).

A "step" in the Late Wisconsinan climatic gradient apparently existed between northern Tennessee and west-central Virginia, producing these zoogeographic patterns. At 10,000 yr BP, the boundary between mixed conifer-northern hardwoods and deciduous forest vegetation types occurred in this area (Delcourt and Delcourt, 1981). North of this "step," some herptiles have been forced southward or out of the Valley and Ridge Province by climatic change since the latest Wisconsinan, while little range adjustment occurred south of the "step."

CONCLUSIONS

Late Wisconsinan herpetofaunas show different, less dramatic Wisconsinan–Holocene range adjustments than the birds and mammals from the same local faunas. No herptiles from these six localities have left the region or are now extinct. Twenty-eight birds and mammals from the combined faunal list are now extirpated from the fossil localities, 17 mammals and one bird are extinct. In 1965 it was possible to state: "The fluctuating ecological conditions during the Pleistocene must have modified the distribution of reptiles more than that of mammals or birds living in the same geographic area" (Auffenberg and Milstead, 1965:557). With the increasing number of herpetofaunas available for study, this view is no longer tenable for eastern North America. Even with the evidence at hand and previous statements (Smith, 1957:207) to the contrary, herptiles that do not match the bird and mammal reconstructions are dismissed in the current literature; ". . . the (Clark's Cave) herpetofauna is similar to that of the area today, with several species . . . that would have been *unable to survive* the 'boreal' conditions postulated for the area on the basis of the mammalian fossil fauna" (Lundelius et al., 1983:316 and 324; emphasis added). There is no evidence for the implication that the herptiles are heterochronic intrusions into the fossil accumulations (Fay, 1984b; Holman, 1986) or that temperate herptiles *must be* ecologically incompatible with "boreal" birds and mammals. In fact, the "boreal" nature of these local faunas may have been over-emphasized. Although many taxa represented by fossils now range further north than the Appalachian localities, no more than 18% of the mammal taxa (at New Paris No. 4, Unit B) are restricted to latitudes north of the central Appalachians.

A number of alternative explanations, several already alluded to in this study,

may be advanced based on zoogeography, taxonomy, and ecology of Appalachian herptiles (Fay, 1986). (1) There are fewer eastern North American boreal herptiles than mammals that could be displaced by glaciation to form a boreal + temperate association. (2) It is apparent from the discussion of plethodontid salamanders that several herptile genera and many species, including relatively "boreal" ones, go unrecognized in the fossil record because of osteological similarity to more widespread taxa. (3) Herptiles did not respond as strongly to glacial-interglacial climatic changes as did other vertebrates. Herptiles have a marked capacity for acclimatization to seasonal climatic change that may also provide the ability to adapt to progressive, long term change by alterations in physiology or behavior rather than distribution. (4) Much of the herpetofauna of the central and southern Appalachians has its center of distribution here, reflecting probable center of origin and/or restricted microhabitat requirements for many of the species. In other words, the animals have endured in suitable local environments since first evolving, in spite of general changes in climate and biota. The southern and central Appalachian region, once thought to be the refugium for the entire eastern temperate biota (Braun, 1950), held individual taxa or enclaves of plants (Davis, 1983a, 1983b). The region also "shielded" the herpetofauna in whole or in part from glacial climates. The preceding statements are not strongly documented as yet, but are intended as directions for further investigations into the neontology as well as paleontology of the Appalachian herpetofauna.

An hypothesis that explains the admixture of faunal elements in Quaternary fossil accumulations that are not now sympatric is that of increased climatic equability compared to the strongly continental climate prevailing over much of North America now. Milder winters are implied, allowing southerly distributed taxa to expand northward, as well as cooler summers permitting northerly distributed taxa to disperse southward (Holman, 1976 and references therein). Although giant tortoises were a stimulus to the development of the hypothesis (Hibbard, 1960), only a few attempts have been made to evaluate climatic equability in regard to the Quaternary herpetofaunal record (Holman 1976, 1977b, 1980).

Rhodes (1984) asserts that it is unnecessary to invoke climatic equability for local faunas containing a greater number of boreal, fewer temperate-mesic, and no more-southern forms than occupy the locality today. Increased microclimatic contrast between slope exposures may have been sufficient to allow range overlaps of boreal and temperate animals. No "southern" mammal component that would indicate milder winters (with possible exception of *Dasypus, Mylohyus, Platygonus,* and *Tapirus,* but see Rhodes [1984] for a dissenting view) occurs in these Late Wisconsinan Appalachian local faunas. Although herpetofaunal sympatry areas are south of three of the six localities of this study, the herpetofaunas contain no true southern (i.e., austroriparian) taxa and the one report of a true boreal taxon *Bufo americanus copei,* is not supported. The only Late Wisconsinan association that includes north and south extralimitals is from Ladds Quarry, Georgia, where *Geochelone* cf. *G. crassus, Pseudemys floridana,* and *Bufo terrestris* occur with *Clemmys insculpta* and *Elaphe vulpina* (Holman, 1985a). If climatic equability can be registered in the herptile record for eastern North America, it decayed to the present continental pattern, with this one known exception, by the end of the Wisconsinan Age. It is not yet clear what special circumstances were responsible for the Ladds faunal composition and if other localities may yield similar associations.

At the end of Wisconsinan time, the vegetation from 34°N to 37°N underwent a major change in species composition as boreal plant taxa removed to the north during glacial retreat (12,500 to 9,000 yr BP; Delcourt and Delcourt, 1983). In the latest Wisconsinan–earliest Holocene interval, deciduous forest in the region of the six herpetofaunas reached its highest species richness during relatively cool, equable conditions (Delcourt, 1979).

While mammalian and avian faunal composition altered to adjust from a full-glacial "boreal" environment with tundra, taiga, and boreal forest species present in the region to a post-glacial environment with deciduous forest, the herpetofauna remained almost undisturbed (with a comparatively minor southward shift of sympatry areas for central Appalachian associations) through over 7,000 years of climatic, vegetational, and faunal change. The climatic and biotic changes were within the tolerance limits of most reptiles and amphibians, and/or when used as proxy data, most herptiles represent local microclimate rather than regional macroclimate (re: Bryson, 1985). Future study must determine what partial analogs may be applied in comparing Quaternary herptiles with the remainder of the fossil record.

LITERATURE CITED

AUFFENBERG, W. 1963. The fossil snakes of Florida. Tulane Studies in Zoology, 10(3):131–216.

AUFFENBERG, W., AND W. W. MILSTEAD. 1965. Reptiles in the Quaternary of North America. Pp. 557–568, in The Quaternary of the United States (H. E. Wright, Jr., and D. G. Frey, eds.), Princeton University Press, 922 pp.

BLAIR, L. O., J. H. HENRY, AND J. M. SNEED. 1981. A preliminary report on the study of Kingston Saltpeter Cave, Georgia. Georgia Journal of Science (abstract), 39(2):66.

BLAIR, W. F. 1965. Amphibian speciation. Pp. 543–556, in The Quaternary of the United States (H. E. Wright, Jr., and D. G. Frey, eds.), Princeton University Press, 922 pp.

BRAUN, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York (1974 reprint), 596 pp.

BRUNNSCHWEILER, D. H. 1962. The periglacial realm in North America during the Wisconsin glaciation. Biuletyn Periglacjalny, 11:15–27.

BRYSON, R. A. 1985. On climatic analogs in paleoclimatic reconstruction. Quaternary Research, 23(3):275–286.

BURY, R. B. 1979. Review of the ecology and conservation of the Bog Turtle, *Clemmys muhlenbergii*. U.S. Department of Interior, Fish and Wildlife Service Special Scientific Report—Wildlife No. 219, 9 pp.

CONANT, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Company, Boston, 429 pp.

COOK, F. R. 1984. Introduction to Canadian amphibians and reptiles. National Museum of Natural Sciences, National Museums of Canada, Ottawa, 200 pp.

COPE, E. D. 1899. Vertebrate remains from the Port Kennedy bone deposit. Academy of Natural Sciences of Philadelphia Journal, 11:193–267.

DANSEREAU, P. M. 1957. Biogeography—an ecological perspective. Ronald Press, New York, 394 pp.

DAVIS, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. Geoscience and Man, 13:13–26.

———. 1983a. Holocene vegetational history of the eastern United States. Pp. 166–181, in Late Quaternary environments of the United States; Volume 2, The Holocene (H. E. Wright, Jr., ed.), University of Minnesota Press, Minneapolis, 277 pp.

————. 1983*b*. Quaternary history of deciduous forests of eastern North America and Europe. Annals Missouri Botanical Garden, 70(3):550–563.

DELCOURT, H. R. 1979. Late Quaternary vegetation history of the eastern Highland Rim and adjacent Cumberland Plateau in Tennessee. Ecological Monographs. 49(3):255–280.

DELCOURT, H. R., AND P. A. DELCOURT. 1983. Late Quaternary vegetational dynamics and community stability reconsidered. Quaternary Research, 19(2):265–271.

DELCOURT, P. A., AND H. R. DELCOURT. 1981. Vegetation maps for eastern North America: 40,000 yr B. P. to the present. Pp. 123–165, *in* Geobotany II (R. C. Romans, ed.), Plenum Publishing Corporation, New York.

DILLON, L. S. 1956. Wisconsin climate and life zones in North America. Science, 123:167–176.

DOWLING, H. G., AND W. E. DUELLMAN. 1978. Systematic herpetology: a synopsis of families and higher categories. HISS Publications, New York, Publications in Herpetology No. 7.

FAY, L. P. 1984*a*. Mid-Wisconsinan and mid-Holocene herpetofaunas of eastern North America: a study in minimal contrast. Pp. 14–19, *in* Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday (H. H. Genoways and M. R. Dawson, eds.), Carnegie Museum of Natural History Special Publication No. 8, 538 pp.

————. 1984*b*. Wisconsinan Appalachian herpetofaunas: what about distributional changes, heterochroneity, and seasonal climatic response? American Quaternary Association 8th Biennial Meeting, Abstracts with Program, p. 42.

————. 1986. Wisconsinan herpetofaunas of the central Appalachians. Virginia Division of Mineral Resources Publication 75:126–128.

FLINT, R. R. 1971. Glacial and Quaternary Geology. John Wiley and Sons, New York, 892 pp.

GRAHAM, R. W. 1985. Diversity and community structure of the late Pleistocene mammal fauna of North America. Acta Zoologica Fennica 170:181–192.

GRAHAM, R. W., AND E. L. LUNDELIUS, JR. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. Pp. 223–249, *in* Quaternary Extinctions: A Prehistoric Revolution (P. S. Martin and R. G. Klein, eds.), The University of Arizona Press, Tucson, 892 pp.

GUILDAY, J. E. 1962. The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia. Annals of Carnegie Museum, 36(7):87–122.

————. 1967. Notes on the Pleistocene Big Brown Bat (*Eptesicus grandis* [Brown]). Annals of Carnegie Museum, 39(7):105–114.

GUILDAY, J. E., P. S. MARTIN, AND A. D. MCCRADY. 1964. New Paris No. 4: a Pleistocene cave deposit in Bedford County, Pennsylvania. National Speleological Society Bulletin, 26(4):121–194.

GUILDAY, J. E., P. W. PARMALEEE, AND H. W. HAMILTON. 1977. The Clark's Cave bone deposit and the Late Pleistocene paleoecology of the central Appalachian Mountains of Virginia. Bulletin of Carnegie Museum of Natural History 2, 86 pp.

GUILDAY, J. E., H. W. HAMILTON, E. ANDERSON, AND P. W. PARMALEE. 1978. The Baker Bluff Cave deposit, Tennessee, and the Late Pleistocene faunal gradient. Bulletin of Carnegie Museum of Natural History 11, 67 pp.

HIBBARD, C. W. 1949. Techniques for collecting microvertebrate fossils. University of Michigan Museum of Paleontology Contributions, 8(2):7–19.

————. 1960. An interpretation of Pliocene and Pleistocene climates in North America. Michigan Academy of Science, Arts, and Letters 62nd Annual Report, 64:5–30.

HOLLAND, W. J. 1908. A preliminary account of the Pleistocene fauna discovered in a cave opened at Frankstown, Pennsylvania. Annals of Carnegie Museum, 4:228–233.

HOLMAN, J. A. 1967. A Pleistocene herpetofauna from Ladds, Georgia. Georgia Academy of Science Bulletin, 25(3):154–166.

————. 1968. Upper Pliocene snakes from Idaho. Copeia, 1968(1):152–158.

————. 1976. Paleoclimatic implications of "ecologically incompatible" herpetological species (Late Pleistocene: southeastern United States). Herpetologica, 32:290–295.

————. 1977*a*. The Pleistocene (Kansan) herpetofauna of Cumberland Cave, Maryland. Annals of Carnegie Museum, 46(11):157–172.

————. 1977*b*. Herpetological evidence for the Pleistocene equability hypothesis in North America. X International Quaternary Congress (abstract), Birmingham, England, p. 211.

————. 1979. A review of North American Tertiary snakes. Michigan State University Museum Publications Paleontological Series, 1(6):200–260.

————. 1980. Paleoclimatic implications of Pleistocene herpetofaunas of eastern and central North America. Nebraska Academy of Science Transactions, 8:131–140.

————. 1981. A review of North American Pleistocene snakes. Michigan State University Museum Publications Paleontological Series, 1(7):263–306.

————. 1982. The Pleistocene (Kansan) herpetofauna of Trout Cave, West Virginia. Annals of Carnegie Museum, 51(20):391–404.

———. 1985a. Herpetofauna of the Ladds Quarry indicates climatic equability in the Late Pleistocene of Georgia. National Geographic Research, 1(3):423–436.

———. 1985b. New evidence on the status of Ladds Quarry. National Geographic Research, 1(4): 569–570.

———. 1986. The known herpetofauna of the late Quaternary of Virginia poses a dilemma. Virginia Division of Mineral Resources Publication 75:36–42.

KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

LUNDELIUS, E. L. 1967. Late Pleistocene and Holocene faunal history of central Texas. Pp. 287– 319, in Pleistocene extinctions: the search for a cause (P. S. Martin and H. E. Wright, Jr., eds.), Yale University Press, New Haven, 453 pp.

LUNDELIUS, E. L., R. W. GRAHAM, E. ANDERSON, J. E. GUILDAY, J. A. HOLMAN, D. W. STEADMAN, AND S. D. WEBB. 1983. Terrestrial vertebrate faunas. Pp. 311–353, in Late Quaternary environments of the United States; Volume 1, the Late Pleistocene (S. C. Porter, ed.), University of Minnesota Press, 407 pp.

LYNCH, J. D. 1966. Additional treefrogs (Hylidae) from the North American Pleistocene. Annals of Carnegie Museum, 38(11):265–271.

MARTIN, P. S. 1958. Taiga-tundra and the full-glacial period in Chester County, Pennsylvania. American Journal of Science, 256(7):470–502.

MARTOF, B. W., W. M. PALMER, J. R. BAILEY, AND J. R. HARRISON, III. 1980. Amphibians and reptiles of the Carolinas and Virginia. University of North Carolina Press, Chapel Hill, 264 pp.

McCOY, C. J. 1982. Amphibians and reptiles in Pennsylvania. Carnegie Museum of Natural History Special Publication 6, 91 pp.

McKENNA, M. C. 1962. Collecting small fossils by washing and screening. Curator, 5(3):221–235.

MEAD, J. I., AND D. J. MELTZER. 1984. North American Late Quaternary extinctions and the radio-carbon method. Pp. 440–450, in Quaternary extinctions: a prehistoric revolution (P. S. Martin and R. G. Klein, eds.), The University of Arizona Press, Tucson, 892 pp.

MEYLAN, P. A. 1982. The squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida). Florida State Museum Biological Sciences Bulletin, 27(3):111–196.

PETERSON, O. A. 1926. The fossils of the Frankstown Cave, Blair County, Pennsylvania. Annals of Carnegie Museum, 16(2):249–314.

RAY, C. E. 1967. Pleistocene mammals from Ladds, Bartow County, Georgia. Georgia Academy of Science Bulletin, 25(3):120–150.

RHODES, R. S., II. 1984. Paleoecology and regional paleoclimatic implications of the Farmdalian Craigmile and the Woodfordian Waubonsie mammalian local faunas, southwestern Iowa. Illinois State Museum Report of Investigations No. 40, 51 pp.

RICHMOND, N. D. 1964. Fossil amphibians and reptiles of Frankstown Cave, Pennsylvania. Annals of Carnegie Museum, 36(20):225–228.

SCHMIDT, K. P. 1938. Herpetological evidence for the postglacial eastward expansion of the steppe in North America. Ecology, 19(3):396–407.

SMITH, P. W. 1957. An analysis of post-Wisconsin biogeography of the Prairie Peninsula region based on distributional phenomena among terrestrial vertebrate populations. Ecology, 38(2):205– 218.

SNEED, J. M. 1981. Paleontological finds at Kingston Saltpeter Cave, Bartow County, Georgia. The Potomac Caver, 24(9):142–144.

SOLER, E. I. 1950. On the status of the family Desmognathidae (Amphibia: Caudata). University of Kansas Science Bulletin, 33(2):459–477.

TIHEN, J. A. 1958. Comments on the osteology and phylogeny of ambystomatid salamanders. Florida State Museum Biological Sciences Bulletin, 3(1):1–50.

VAN DAM, G. G. 1978. Amphibians and reptiles. Pp. 19–25, in The Baker Bluff Cave deposit, Tennessee, and the Late Pleistocene faunal gradient (J. E. Guilday, H. W. Hamilton, E. Anderson, and P. W. Parmalee, eds.). Bulletin of Carnegie Museum, 11, 67 pp.